Food finding

Prop, Jouke

Chapter 13

Survival costs related to the timing of breeding and brood size in Arctic barnacle geese

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Abstract

In many animals, reproduction results in a lower probability of survival but often the mechanism of this cost of reproduction is difficult to assess. This study on the high-Arctic barnacle goose *Branta leucopsis* aimed to test if any survival costs were associated with the timing of reproduction or with the timing of other functions later in the year, which could be due to incompatible time schedules. Survival rates of adults were related to breeding status, timing of breeding and reproductive effort (including brood size) from resightings of 179 marked individuals, followed over a four-year period both in the breeding area and in winter. In females, non-breeders survived better than failed breeders, which tended to have a higher survival than successful breeders (0.95±SE 0.029, 0.86±0.032, 0.82±0.041, respectively). In males annual survival did not differ significantly by breeding status (0.94±0.033, 0.82±0.038, 0.92±0.025). Survival in summer through autumn migration was negatively correlated with the timing of breeding. Most variance in survival was explained by the date of nest departure (i.e. date of hatch and of nest desertion for successful and failed breeders respectively) suggesting that environmental conditions after incubation determined the probability of survival. The seasonal decline of food quality (protein content) documented in the study area provides a potential mechanism accounting for lower survival of late breeders when taken in conjunction with the limited time available for pre-migratory deposition of body stores. Larger broods had a more negative effect on survival of female parents than was the case in males, and may be caused by sex-related risks of predation by Arctic foxes. This study supports a strong selection against late breeding, as documented by previous studies. Strikingly, this study suggests that there is a selection in favour of early abandoning the nest, in case individual body stores are mismatched to local foraging opportunities. This may be a general strategy for long-lived species that face a large annual variation in conditions to hatch the eggs successfully.

Submitted

Introduction

One of the central issues of life history theory is concerned with the 'costs of reproduction' (Stearns 1992). Costs are predicted to arise because of a trade-off between current and future reproduction, and may include a reduction in future fecundity or in the probability of survival to the next breeding attempt (Williams 1966). Costs may have several sources, most notably those arising from competitive allocation of resources ('physiological costs', Reznick 1992). For example, a cost is involved when an animal invests in a large brood at the expense of its own survival (Nur 1988, Daan *et al*. 1990). Similarly, reproduction and moult are among the time and energy consuming events in the annual cycle of birds (Farner *et al*. 1980), and therefore fitness costs associated with the timing of breeding arise when the length of the season is short (Orell and Ojanen 1980, Siikamaki *et al*. 1994). Thus, Dhondt (1981) postulated that a decrease in survival rate with breeding date observed in great tits was a consequence of late-breeding birds failing to complete the moult. A negative relationship of survival with breeding date has also been observed in several other studies (Nur 1984, Verhulst *et al*. 1995, Nilsson and Svensson 1996, Wiggins *et al*. 1998, in contrast to Brown and Brown 1999), but the exact mechanism of this relationship remains obscure. This is largely due to difficulties in following the birds' performance after fledging, when most of the mortality occurs (Newton 1998).

We studied survival rates in a barnacle goose *Branta leucopsis* population that breeds in high-arctic environments (Spitsbergen), and we aimed to identify survival costs associated with breeding. The restricted distribution during the different phases in the annual cycle (Owen 1980a) makes intensive reading of individual leg rings possible for much of the year, which allows to obtain estimates for survival for seasonal periods (Owen 1982). For four successive years we recorded the breeding performance of birds in a large breeding colony, which enabled us to compare survival rates of birds of different breeding status (non-breeders, failed and successful breeders). Moreover, we determined the dates of onset of egg-laying and when birds started to moult relative to dates of nest loss (failed birds) or hatch (successful birds). We tested if differences in survival rates associated with breeding status were related to the timing of breeding or to the timing of moult. Given the large impact of food quality on body reserves dynamics in herbivores like geese (Robbins 1993), we measured crude protein content of the food throughout summer to interpret the implications of timing of breeding and moult on survival probabilities. As brood size and timing of breeding are confounded life history traits (Wiggins *et al*. 1998), we checked for effects of brood size on survival.

Methods

Study population

The study population of barnacle geese breeds in Spitsbergen, which requires a 3000 km migration to and from the wintering area in the Solway Firth area, UK (Fig. 1). In

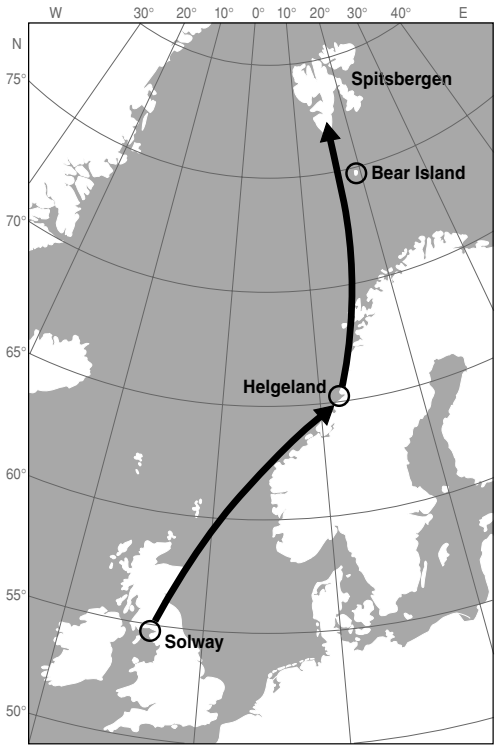

Fig. 1. Map of the spring migration route of the study population. Indicated is the study area in Spitsbergen and the centre of the wintering area at the Solway (UK), the staging area in Helgeland (Norway), and Spitsbergen (breeding area). The autumn route is in the opposite direction with no or only a brief stop along the Norwegian coast, but instead with a stay on Bear Island (Owen and Gullestad 1984).

a long-term population study individuals were supplied with coded leg rings that were readable at a large distance (Owen 1982). Ring resightings formed the basis for the survival estimates. The 179 individuals followed during this study had been ringed in the summer preceding the study period or in earlier years in the wintering area. We collected data during two stages of the annual cycle: in a colony of approximately 150 pairs at the west coast of Spitsbergen (Diabasøya; 77º50'N 13º45'E; Prop and De Vries 1993) in 1978 through 1981, and in the Caerlaverock Nature Reserve, Scotland (54º58'N 3º30'W, Owen *et al*. 1987), in 1978 through 1982. The resighting rate was so high that further corrections from sightings in later years are not relevant (see below). During each season we obtained a large number of resightings for most of the marked individuals if still alive. The high intensity of reading was due to the large site loyalty to the breeding colony, a feature of geese in general (Ganter and Cooke 1998, O'Briain *et al*. 1998), and the restricted wintering range, with almost the whole population visiting the study location. Both in summer and winter we used tall observation towers that provided perfect view on the geese.

The study area in Spitsbergen is a strandflat composed of Polar semi-deserts and High Arctic landscapes (Bliss 1981), consisting of quaternary marine deposits with raised marine terraces and beach ridges and slightly elevated Precambrian formations (up to 40 m above sea level), covered by a 'fjellmark' vegetation (Elveback 1985). The geese nest mainly in three larger colonies, from where they disperse to shallow lakes for brood-rearing and moulting (Prop *et al*. 1984). Non-breeders and failed-breeders use the same lakes to moult but being earlier than successful geese, they are in some years more restricted in choice due to ice cover. Main food plants around the lakes are graminoids (*Dupontia pelligera*, *Poa arctica* and *Festuca rubra*.). As soon as the geese regain the power of flight they leave the moulting lakes, and they have 3-6 weeks left to prepare for the autumn migration. During this time they mainly use the fjellmark to feed on a large variety of plants, including *Equisetum variegatum*, fruits of *Saxifraga* spp., and bulbills of *Polygonum viviparum*. From the end of August onwards the geese move to lush river valleys inland, and in particular after the first snow they use slopes beneath seabird cliffs feeding on grasses (*Alopecurus borealis*, *Poa arctica*). Goose migration to the south occurred from mid September onwards, usually following heavy snowfall and low temperatures (Prop *et al*. 1984). Most of the birds seem to pass through Bear Island on their way to the wintering grounds (Owen and Gullestad 1984).

Reproduction

To establish which pairs initiated breeding we recorded the behaviour of the birds during the process of occupying a territory and clutch completion. We called a pair to have initiated breeding when occupying the same nest location for at least two days. When hatching at least one egg, pairs were called successful, as opposed to failed breeders that lost the clutch before hatching the eggs. Dates of hatching the eggs, or of abandoning the nest (collectively called dates of departure) were recorded for all ringed pairs. Successful birds required 30 days for egg laying and incubation (Prop and De Vries 1993), which means that dates of nest initiation and hatch were closely correlated. In contrast, failed birds showed a wide range between the dates of nest initiation and abandoning the clutch (see Results). By definition, non-breeders did not occupy a territory, but occasionally they produced eggs (stray eggs or dumped in the nest of an other goose pair). By continuously observing the breeding colony brood sizes were determined at the time of hatch. Thereafter, intensive observations of the marked pairs and their goslings on the brood raising grounds enabled us to keep track of brood sizes through time. Glaucous gulls *Larus hyperboreus* and Arctic foxes *Alopex lagopus* predated on the goslings, and as an average brood size we took the number of young at 1 August, which coincided with the begin of moult of the primaries (hereafter called moult) by the parents. Broods of zero included pairs that had lost all their young before the moult and failed breeders.

Moult

To establish when geese moulted in relation to the date of hatch we noted when marked individuals with known breeding history lost the first wing feathers. Because males and

females moult, on average, simultaneously (Owen and Ogilvie 1979), dates of begin of moult were averaged per pair. Likewise, we kept track of the dates when birds regained power of flight later in summer. Non-breeders, together with early failed breeders (see Results), moulted on lakes where they aggregated a few days before the first birds actually started to moult. Progress of moult was determined by daily counts of the number of moulting birds. In a similar way we determined the end of the moulting period. Assessing which individuals were able to fly was facilitated by frequent disturbances caused by Arctic foxes. For each year, median dates of begin and end of moult were calculated.

Food samples

To determine the quality of food throughout summer, samples of food plants were collected. The samples were dried at 60ºC and stored for later processing. Plants were collected whenever representative for the diet during successive stages in summer. Later in the laboratory, samples were ground to pass a 1 mm sieve and analysed at total nitrogen (Kjeldahl). To arrive at a standard measure of food quality crude protein (hereafter protein) was calculated as 6.25 times the nitrogen dry weight content (Robbins 1993).

Survival analysis

Survival rates were calculated on the basis of resightings of ringed birds from the first observation in the breeding colony onwards. We eliminated the few individuals from the data set that were known to nest in other nearby colonies (based on observations during brood rearing) and that usually were only reported as non-breeder in the study colony. Likewise, we restricted analyses to birds older than 3 years to avoid heterogeneity in the data by potential age effects (Owen 1982, Van der Jeugd and Larsson 1998). When both mates of a pair carried rings we selected, on a random basis, one of the two birds for analyses to avoid pseudoreplication (Schmutz *et al*. 1995). We dealt with two focus periods of observations: the incubation period in summer in Spitsbergen (early June-mid July), and the autumn in the wintering area at the Solway Firth (October-early December). This allowed to consider survival for two seasonal periods: summer to autumn (hereafter 'summer'), which included the brood rearing period and autumn migration; and autumn to summer (hereafter 'winter'), which included the wintering season in Britain, the spring staging period in Norway and spring migration. Annual values were calculated from one summer to the next. We analysed 179 individual encounter histories, with effective sample sizes of 391 (on an annual basis, 3 intervals) and 862 (by season, 7 intervals).

We estimated survival rates by the Cormack-Jolly-Seber (CJS) procedure using the program MARK (White and Burnham 1999). On the basis of the resighting histories both survival rates (Φ) and resighting probabilities (p) were calculated. Survival rates were related to the time of breeding and brood size. Because these covariates were scored as missing values in the years that individuals did not breed, a straightforward CJS approach was not possible. More elaborate models (multi-strata analysis, Nichols and Kendall 1995) can cope with our sort of data and are to be preferred, but the restricted

sample sizes disqualified their use. Instead, we chose to analyse the relationships between survival and breeding parameters by logistic regression. This regression does not account for resighting probabilities, and therefore we adjusted resighting histories in cases that individuals were not observed at the second occasion of an interval, but which were known to be alive on the basis of observations in later seasons. This adjustment does not cover individuals that were still alive at the second occasion without being ever reported, but we think this introduced only a negligible bias in the estimates for the following reasons. Given the survival rates and resighting probabilities in this study (see Results) survival rate based on logistic regression was underestimated by less than 0.002, and, most important, there is no reason to suspect any effect on trends reported. The estimates of survival probabilities in this study likely represent true survival. This is due to the strong site fidelity of the geese, and because we collected data both in the summer and in the winter range thus avoiding the complication of local emigration.

As a first step in the analysis, sets of candidate models were chosen on the basis of the biology of the geese (Anderson and Burnham 1999), with the global model for each set including all relevant parameters. First, we examined the effect of breeding status (non-breeding, failed or successful breeder) on annual survival rates, while controlling for sex and year. The status in each of the years was defined by two dummy covariates, totalling to eight variables for four observation years. Resighting probabilities were tested for effects of year type and of breeding status. The two year types distinguished were early and late snow melt years, as we knew that less geese started incubating in late years (Prop and De Vries 1993), which we suspected to affect resighting rates. We tested resighting rates for the breeding status in the preceding year as we expected that the outcome of breeding affected the decision to return to the breeding colony the next year. When modelling survival rates we assumed that effects of sex and status were constant over time and therefore no interaction terms with year were included. To this end, the four dummy variables indicating successful breeding in successive years were constrained to estimate only one parameter, and the four variables indicating failed breeding were treated similarly.

Subsequently, we compared survival rates between the two seasons (Ward *et al*. 1997). Resighting rates were tested for season-effects by distinguishing between the first winter, when the effort to read rings was lower than in any other season, the two late snow melt summers, and all other seasons. Also in this analysis we tested for the effect of breeding status on resighting probabilities. Models of survival rates included all two-way interaction terms (status × sex, status × season, sex × season) or more reduced models.

As a following step in the analysis of seasonal survival rates we added parameters associated with timing of breeding (dates of nest initiation and nest departure) and with breeding effort (brood size). The global model included year, sex and the breeding parameters (status, brood size, date of nest initiation and date of nest departure). Status and brood size were tested for differences between the sexes (status × sex and brood size × sex), and no other interaction terms were included. All reduced models were compared, but interaction terms were only included in combination with the variables as main effect.

Model selection

Model selection followed Lebreton *et al*. (1992) and Anderson and Burnham (1999). Goodness of fit tests (by program RELEASE in MARK) were performed for the global models to test for equal resighting and surviving probabilities for all individuals in the samples. The global models appeared statistically acceptable for the data considered ($P>0.5$ in all cases), which means that further modelling was justified (Lebreton *et al*. 1992).

Model selection aimed to detect the most parsimonious model, i.e. the number of parameters was reduced to have a model that still provided a good representation of the data. All candidate models were ranked on the basis of the Akaike's Information Criterion (AICc) with a correction for sample size. AICc was calculated as $-2\ln(L) + 2NP + 2NP \times (NP + 1)/(N - NP - 1)$, where L is the model likelihood, $-2\ln(L)$ is the deviance, NP is the number of parameters, and N is the effective sample size. The AICcWeight provides a way to calibrate the models investigated against each other, all weights of the candidate models summing up to 1. To test for effects of single parameters the 'best' model was tested with reduced ones using likelihood ratio tests (Lebreton *et al*. 1992). Starting with the global model we first modelled resighting probabilities. Subsequently, the resulting parameter set for the resighting probabilities was used in further modelling survival rates (Lebreton *et al*. 1992).

Unless otherwise stated, data are reported as average values ± standard error of the mean (*SE*).

Results

Timing of reproduction and moult

Nest initiation took place on average at 9.3±0.28 June, successful pairs being 2.9 days earlier than failed pairs ($F_{1,514}=4.15$, $p<0.05$ while controlling for year-effects). Hatch dates averaged at 7.9±0.32 July. The date of nest departure for failed breeders was almost 8 days earlier at 30.2±0.67 June. Individuals that initiated a nest late required less time for egg-laying and hatching the clutch (Fig. 2), although the compensatory effect was small (given the slope of the regression, the reduction in incubation time with later dates of nest initiation was 10%). Similarly, the egg-laying and incubation period of failed breeders declined with date of settling.

Non-breeders started to moult the primaries at on average 6 July (Fig. 3), with the annual median values ranging from 3-10 July. They regained the power of flight 27 days later, on average on 2 August. Successful birds showed a strong correlation between the dates of moult and nest departure ($y=19.5+0.87x$, $F_{1,15}=52.8$, $p<0.0005$), and they began moulting on average 14.6 ±0.44 days after hatching the eggs (Fig. 4). As the slope of the regression between the date of moult initiation and date of hatch did not deviate from 1 (the 95% confidence interval was 0.62-1.13), we conclude that birds did not compensate for late hatching. In contrast, failed birds compensated for a late nest departure by moulting earlier (the slope of the regression of dates of moult and of nest departure was 0.67 with a 95% confidence interval of 0.52-0.81). However, this relationship

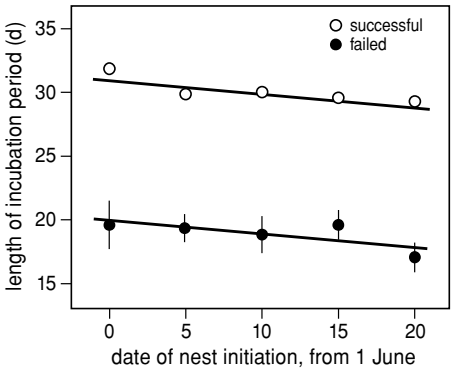

Fig. 2. The duration of incubation (egg-laying inclusive) in relation to the date of nest initiation, for failed and successful breeders separately (average ±SE). The slope of the regression is -0.106, $F_{1,435}$=5.70, p<0.025; the effect of breeding status is -10.88, $F_{1,435}$=394.26, p<0.0005. The slopes of the regressions are similar, $F_{1,434}$=0.00, n.s.

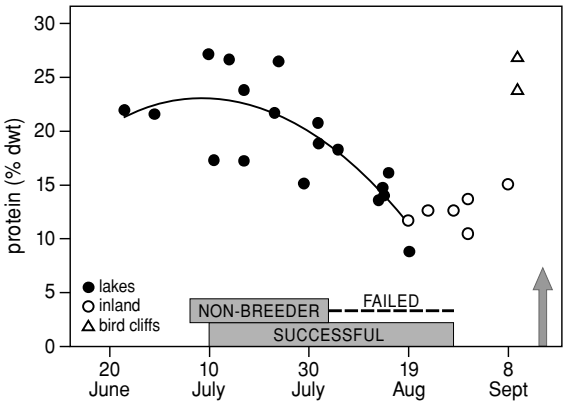

Fig. 3. Protein content of food plants used by geese during the moult (solid circles: y=12.6+0.54x-0.007x^2, $F_{2,15}$=12.7, p=0.001), and after the moult at inland sites (open circles) and at seabird colonies (triangles). The four-years average flightless period for successful birds and non-breeders is given at the bottom. As indicated by the dashed line failed breeders may complete moult simultaneously with non-breeders or as late as successful birds. Start of migration is given by the arrow.

was largely determined by birds that abandoned the nest early in the season. Failed birds that abandoned the nest after 21 June (i.e. the date of start of moult for non-breeders, 6 July, minus 14.6 days) fitted the line generated by successful birds well (test for similar slopes $F_{1,22}$=0.31, non-significant), whereas earlier failed birds moulted simultaneously with the early moulting non-breeders. We thus conclude that the timing of moult was related to the date of nest departure, irrespective whether birds were successful or failed to hatch the clutch.

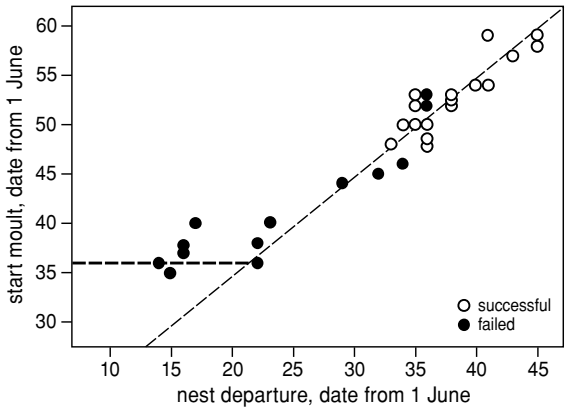

Fig. 4. Relationship between the timing of moult and the date of nest departure. The dashed line assumes a constant interval of 14.6 days between nest departure and start of moult (see text). Pairs losing the clutch after 22 June faced a progressive delay in moult compared to non-breeders (average begin of moult indicated by the horizontal line).

Successful birds were able to fly and left the brood rearing lakes 48 days after hatching the eggs, which means that they stayed flightless for 48-14.6=33.4 days. This is approximately 6 days longer than non-breeders required for the wing moult. However, the shortest moult period observed for parents was 27 days, which suggests that some families stayed longer at the brood rearing sites to synchronize departure with later hatching families.

Food quality through time

Non-breeders and early-failed breeders started to moult when the quality of grasses was close to a peak (23% protein dry weight, Fig. 3) and regained the power of flight when protein levels started to drop (18% in early August). Similarly, hatching took place during the time of peak protein levels, but because of the delayed moult successful birds regained power of flight as late as when protein levels had dropped to a level of 10%. Obviously, late-hatching individuals faced lower protein values throughout the moult, on average, than early-hatching or non-breeding birds. After the moult, when the geese were no longer bound to lakeshores and instead exploited the vast fjellmark, geese cropped plants that contained a larger proportion of protein (Fig. 3), and also more soluble carbohydrates (Prop and Vulink 1992), than the grasses at the moulting sites. Also the grasses on the slopes of seabird cliffs, which the geese visited at the end of the summer, were exceptionally nutritious with high protein concentrations.

Breeding status and survival rate

Resighting probabilities in Spitsbergen did not differ between early and late snow melt years, nor could we detect an effect of breeding status in the previous year on the probability to resight an individual (model 4 in Table 1). In further modelling we assumed

therefore a constant resighting probability p over years and among breeding status (p=0.969±0.011). The annual survival rate was on average 0.872±0.014, and differed by breeding status (χ^2=8.1, df=2, p<0.02). Non-breeding birds survived better than successful and failed breeders, which was true for both sexes as there was no support for an additive sex effect (model 13 versus 8 in Table 1, χ^2=0.2, df=1, n.s.), nor for the interaction between status and sex (model 13 versus 7 in Table 1, χ^2=4.39, df=3, n.s.; see Table 3 for estimates).

When considering seasonal survival, resighting probabilities were invariably high (on average 0.955±0.009) but differed among the three season classes distinguished (model 1 versus 3 in Table 2, χ^2=48.64, df=2, p<0.0001): in the first winter p=0.864, in late springs p=0.960 and in other seasons p=0.991. Moreover, the probability to identify a bird depended on the breeding status (model 1 versus 2 in Table 2, χ^2=34.85, df=2, p<0.0001), with probabilities highest for successful birds (0.993), lowest for non-breeders (0.908), and intermediate for failed breeders (0.955). Seasonal survival rates differed among breeding status (model 19 versus 21 in Table 2, χ^2=7.86, df=2, p<0.05; see Table 3 for the estimates). Survival rates were similar in summer and winter (model 17 versus 19, χ^2=0.14, df=1, n.s.), which was irrespective of the status concerned (models 14 and 17, χ^2=3.84, df=2, n.s.).

Table 1. Models of annual survival Φ and resighting probability p. **A** Modelling p with a constant model for Φ; **B** Modelling survival rate with an average p. Between brackets the parameterisation of Φ and p. NP= number of parameters; year2= years classified by early and late snow melt; status=breeding status. Best model is in bold.

	Model	AICc	Delta AICc	AICc weight	NP
A					
4	**Φ (year+sex×status) p(.)**	385.23	0.00	0.389	9
3	Φ (year+sex×status) p(year2)	386.40	1.17	0.217	10
1	Φ (year+sex×status) p(year2+status)	386.44	1.21	0.212	12
2	Φ (year+sex×status) p(status)	386.75	1.52	0.182	11
B					
12	**Φ (status)**	380.35	0.00	0.419	4
8	Φ (sex×status)	382.15	1.80	0.170	7
7	Φ (sex+status)	382.20	1.85	0.166	5
9	Φ (year+status)	383.60	3.25	0.083	6
13	Φ (.)	384.38	4.03	0.056	2
4	Φ (year+sex×status)	385.23	4.88	0.037	9
5	Φ (year+sex+status)	385.46	5.10	0.033	7
10	Φ (sex) p(.)	386.17	5.81	0.023	3
11	Φ (year) p(.)	387.81	7.45	0.010	4
8	Φ (year+sex)	389.60	9.25	0.004	5

Table 2. Models of seasonal survival Φ and resighting probability p. **A** Modelling p with a constant model for Φ; **B** Modelling survival rate with constant p (season3+status). Between brackets the parameterisation of Φ and p. NP= number of parameters; season3= seasons classified into 3 groups; status=breeding status. Best model is in bold.

	Model	AICc	Delta AICc	AICc weight	NP
A					
1	**Φ (sex×status×season) p(season3+status)**	729.77	0.00	1.000	15
2	Φ (sex×status×season) p(season3)	760.48	30.71	0.000	13
3	Φ (sex×status×season) p(status)	774.27	44.50	0.000	13
B					
18	**Φ (status)**	725.96	0.00	0.227	8
11	Φ (sex×status)	727.04	1.08	0.133	11
14	Φ (sex+status)	727.93	1.98	0.085	9
16	Φ (season+status)	727.94	1.99	0.084	9
5	Φ (status×season+sex×status)	727.98	2.02	0.083	14
13	Φ (status×season)	728.20	2.24	0.074	11
6	Φ (status×season+sex×season)	728.63	2.67	0.060	13
7	Φ (season+sex×status)	729.06	3.10	0.048	12
20	Φ (.)	729.75	3.79	0.034	6
1	Φ (sex×status×season)	729.77	3.81	0.034	15
10	Φ (sex+season+status)	729.92	3.96	0.031	10
9	Φ (sex+season×status)	729.96	4.01	0.031	12
4	Φ (sex×season+sex×status)	730.39	4.43	0.025	13
8	Φ (status+sex×season)	731.06	5.10	0.018	11
19	Φ (season)	731.64	5.69	0.013	7
17	Φ (sex)	731.70	5.75	0.013	7
15	Φ (season+sex)	733.60	7.64	0.005	8
12	Φ (sex×season)	734.70	8.75	0.003	9

Table 3. Estimates of survival rates based on model 7 in Table 1 (annual rates), and model 12 in Table 2 (seasonal rates). Given are the means values ±1SE.

Females	non-breeding	failed	successful
summer	0.957 ±0.021	0.939 ±0.019	0.918 ±0.033
winter	0.987 ±0.022	0.935 ±0.028	0.881 ±0.030
annual	0.953 ±0.029	0.861 ±0.032	0.817 ±0.041
Males	**non-breeding**	**failed**	**successful**
summer	0.963 ±0.024	0.920 ±0.031	0.960 ±0.020
winter	0.990 ±0.025	0.918 ±0.027	0.954 ±0.016
annual	0.940 ±0.033	0.824 ±0.038	0.922 ±0.025

Timing of reproduction, brood size and survival rate

The most parsimonious model explaining seasonal variation in survival rates contained, besides year and sex, three parameters associated with breeding parameters: brood size, brood size×sex, and the timing of nest departure (model 2 in Table 4). The model including status (model 1) had a lower AICc but the status effect was not significant (models 1 versus 2, χ^2=2.51, df=1, n.s.). There was little support for any of the models containing the date of nest initiation (like models 3 or 4). Subsequently we compared the parameters of the best model between seasons (Table 5). The effect of brood size on survival was similar in summer and winter (Table 5). The slope of the regression of survival on brood size was more negative in females than in males (Table 5), but for each sex separately

Table 4. Modelling seasonal survival rates by logistic regression, and testing effects of timing of breeding and brood size. NP= number of parameters; status=breeding status; bs= brood size; depart= date of nest departure; init=date of nest initiation. Best model is in bold.

	Model	AICc	Delta AICc	AICc weight	NP
1	Φ (year+status+bs×sex+depart)	273.93	0.00	0.208	9
2	**Φ (year+bs×sex+depart)**	274.38	0.45	0.156	8
3	Φ (year+status+bs×sex+init+depart)	275.24	1.32	0.107	10
4	Φ (year+bs×sex+init+depart)	275.56	1.63	0.092	9
5	Φ (year+status×sex+bs×sex+depart)	275.98	2.06	0.074	10
6	Φ (year+status+bs×sex+init)	276.88	2.95	0.047	9
7	Φ (year+bs×sex+init)	277.26	3.33	0.039	8
8	Φ (year+status×sex+bs×sex+init+depart)	277.32	3.39	0.038	11
9	Φ (status+bs×sex+depart)	278.15	4.22	0.025	6
10	Φ (year+status×sex+bs+depart)	278.52	4.59	0.021	9
11	Φ (year+bs×sex)	278.59	4.67	0.020	7
12	Φ (year+status×sex+depart)	278.85	4.92	0.018	8
13	Φ (year+status×sex+bs×sex+init)	278.92	5.00	0.017	10
14	Φ (bs×sex+depart)	279.03	5.11	0.016	5
15	Φ (year+status×sex+bs+init+depart)	279.96	6.04	0.010	10

Table 5. Modelling seasonal survival rates by logistic regression, and testing effects of timing of breeding and brood size between seasons. NP= number of parameters; status=breeding status; bs= brood size; depart= date of nest departure; init=date of nest initiation; season=summer or winter. Best model is in bold.

	Model	AICc	Delta AICc	AICc weight	NP
1	**Φ (year+bs×sex+depart×season)**	265.08	0.00	0.984	10
2	Φ (year+bs×sex+depart)	274.38	9.30	0.009	8
3	Φ (year+bs×sex+depart+season)	276.63	11.55	0.003	9
4	Φ (year+bs×sex+depart+sex×season)	278.32	13.24	0.001	10
5	Φ (year+bs×sex+depart+bs×season)	278.50	13.42	0.001	10
6	Φ (year+bs×sex+depart+bs×sex×season)	278.67	13.59	0.001	10

the regressions were not significantly different from zero (in females the slope was -0.327±0.178, p=0.065; in males 0.387±0.285, p=0.175; Fig. 5).

In contrast, the timing of nest departure affected survival rates differently in summer and winter (Table 5). In summer, survival rates were negatively related to date of nest departure (the slope of the regression was -0.156±0.046, p<0.0005), whereas the survival in winter was not correlated with date of nest departure (the slope of the regression did not differ from zero, 0.047±0.042, p=0.096) (Fig. 6).

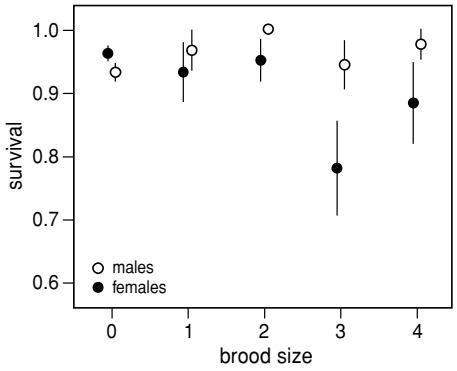

Fig. 5. Seasonal survival rates for males and females in relation to brood size. Given are the observed means and SE. None of the trends are significant (see text). The 0-class includes individuals that lost the clutch (failed breeders) or that lost all their goslings before 1 August.

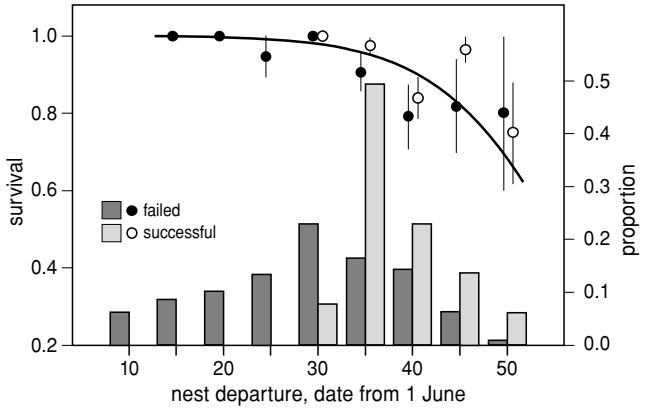

Fig. 6. Seasonal survival rate (summer only) in relation to the date of nest departure for failed and successful birds separately. Given are the observed means and SE. The curve is derived from model 1 in Table 5: y=11.67-0.156x (on a logit scale); χ^2=12.22, df=1, p<0.0005. For comparison, the frequency distributions of the dates of hatch (successful individuals) and dates of abandoning the nest (failed) are given (right y-axis).

Discussion

This study provided support for a 'cost of reproduction' in barnacle geese by a gradient in survival rates: non-breeders survived better than breeding birds, and failed breeders tended to have a higher survival rate than successful birds. We identified two life history traits that were associated with this gradient. In the first place the probability to survive declined with progressive dates of nest departure, which was independent of whether the clutch was successfully hatched or not. Thus, successful birds, which usually departed the nest at later dates than failed breeders, faced a stronger time-disadvantage. Secondly, females producing large broods tended to survive less well than birds with small broods or without any offspring.

Survival and timing of breeding

The consequence of the timing of breeding on the survival rates of the offspring has gained wide interest in avian studies (e.g. Perrins 1970, Newton and Marquiss 1986). In contrast, repercussions of the timing of breeding on parental survival have been studied relatively little, and the few studies available showing both negative (Nur 1984, Wiggins 1991, Verhulst *et al*. 1995) and positive trends (Brown and Brown 1999). In the first

After geese departed from Spitsbergen, vegetation transects are sampled for a last time.

place, a trend in quality of individuals may affect any trend in survival (Verhulst *et al*. 1995, Brinkhof and Cave 1997). We did not perform experiments to test if this was the case in our study species, but we think it is unlikely that the trends in survival observed were caused to any major extent by shifts in bird quality for the following reasons. If a date-dependent survival was primarily due to shifts in bird quality, we would expect, in line with studies on survival of offspring (Brinkhof *et al*. 1997), a negative relationship with date of nest initiation. However, the observations were not consistent with this, as survival was related to date of settling in successful birds, but not in failed breeders. If, for some reason, the quality of failed individuals was not related to the date of settling, but to the date of departure, we would expect a positive relationship between the date of departure and survival (assuming that low-quality birds abandon the nest first), which also was not supported by the observations.

Instead, survival rates in successful and failed birds fit the interpretation of a close relationship with the dates of nest departure. We envisage a causal relationship between survival and the timing of breeding, as dates of nest departure determined when the birds started to moult (Fig. 4), which we suggest as a key factor to understand the patterns in survival observed. Below we argue that a late moult negatively affected the prospects to accumulate sufficient body stores required for a successful migration to the wintering area (Owen and Black 1989b), or that a late moult made the geese more vulnerable to predation by Arctic foxes. First, the food available for moulting birds showed a continuous decline in quality through summer (Fig. 3), as corresponding to an almost universal pattern in plant phenology (McCown 1978). As a consequence, and in parallel to late hatched goslings (Sedinger and Raveling 1984, Prop and De Vries 1993, Lindholm *et al*. 1994), adult birds that moulted late faced, on average, a poor food supply. Although it has been argued that geese do not experience a nutritional bottleneck during moult (Ankney 1984, Hohman *et al*. 1992, in contrast to Owen and Black 1989b, Fox *et al*. 1998), the low-protein diet of late-moulting birds must mean a selective disadvantage. To achieve the same intake of energy and nutrients of early moulters, late-moulting individuals must have spent more time foraging. Or, as an alternative possibility, the late moulters could have been as active as early moulters but then they would experience a lower body condition at the end of the moult. The first strategy would make them more vulnerable to predation by Arctic foxes during the moult (Prop and De Vries 1993); the second would give them a disadvantage for pre-migratory deposition of body stores. Another negative aspect of moulting late is that a low-protein diet may cause a deficit of amino acids required for feather synthesis, which could impair the quality and length of the new feathers (Pehrsson 1987).

Secondly, the pre-migratory period available was shorter with later completion of the moult. Bids that regained the power of flight at 20 August for example had only 25 days available for pre-migratory deposition of body stores. This is a short period considering that during this time the daylight period decreased from 24 hours to slightly more than 12 hours, and concurrently the time available for foraging decreased steeply. The problem is exacerbated by an increasing incidence of snow cover. This means that a later begin of the pre-migratory phase becomes increasingly difficult to compensate for.

A conclusion of this study is that events early in the reproductive cycle have repercussions on the fate of individuals much later in the year (see also Daan *et al*. 1996). Thus, the timing of initiating a nest determined the chance of an individual to reach the wintering grounds during the next autumn. The reason is the rather fixed amount of time required for each of the successive steps in the annual cycle, i.e. incubation, pre-moult, and moult. An earlier start of breeding is constrained by snow conditions early in the season when geese arrive in the breeding area (Prop and De Vries 1993), and probably even earlier by the foraging conditions on the spring staging grounds when the geese deposit pre-migratory body stores (Prop *et al*. 2003). Opportunities to compensate for a late start in the reproductive cycle appeared to be restricted. Thus, the length of the egg-laying and incubation period decreased only slightly with the date of nest initiation (in line with Dalhaug *et al*. 1996). Nor did we find a compensation for a late nest departure by an earlier onset of moult. However, individuals may escape from the rigid time schedule by abandoning the nest. A late breeder may thus become an early moulter, without offspring in the current year but with better prospects for another chance the following years.

Survival and brood size

In contrast to altricial birds, in which reproductive costs (adult survival) are commonly associated with brood size (e.g. Nur 1984, Reid 1987, but see Gustafsson and Sutherland 1988), effects of brood size on parental performance in precocious birds are less obvious. In this respect our finding that survival was correlated with brood size is surprising, although we are not able to tell whether survival was positively related with brood size in males, or negatively in females. In previous studies on geese, no effect of brood size on parental survival was demonstrated (Williams *et al*. 1994 in lesser snow geese *Anser caerulescens*, Lessels 1986 in Canada geese *Branta canadensis*, and Loonen *et al*. 1999 in barnacle geese), which we attribute to other mortality factors operating (the first two populations are severely hunted) and to limited sample sizes (the latter study). Large families are dominant over small families (Black and Owen 1989b), and females, not males, with a large brood are in a better body condition than those raising a small brood (Loonen *et al*. 1999). It seems unlikely therefore that the relatively lower survival of females with large broods was due to a 'physiological cost of reproduction'

(Reznick 1992). We cannot exclude the possibility that females with large broods were more susceptible to predation than females with few offspring or than males, but further study is required to solve this issue.

Reproductive decisions

Life history theory predicts a balance between current investment in offspring and future reproduction (Stearns 1992). This implies that birds should not sacrifice their own survival to raise a brood, if they can raise more offspring in future, a point particularly relevant for long-lived birds like geese. Our study shows that the worst scenario for barnacle geese is to lose the clutch at a late date, thus gaining no offspring and additionally suffering the cost of a decreased probability of surviving. Indeed, as many as 35% of all failed pairs abandoned the nest early enough to enable them to moult simultaneously with non-breeders (before 22 June, Fig. 6), and the majority of the failed-breeders (62%) stopped incubating before the peak hatch. Only 22% of all failures occurred after 10 July when the probability to survive started to drop severely. This means that most pairs were 'choosing' to abandon the clutch before they would suffer the repercussions of a late nest departure. Comparing the survival rate associated with the average date of hatch and the average date of nest desertion (Fig. 6) shows an average gain in survival for the deserting individuals from 0.933 to 0.980 (=+0.047).

There are many ways to minimize the costs of reproduction, for example by feeding the offspring at a low rate (Hsu *et al*. 1999), or by a deferred age of breeding (Ens *et al*. 1995). Likewise, abandoning a clutch in time, when the prospects for successful hatching become poor, can be regarded as a strategy to avoid a cost of reproduction. We can only speculate about the mechanism of how a pair decides to abandon its nest, but it must include interactions between body condition of the geese (Tombre and Erikstad 1996) and the foraging return. This study provided evidence that the survival costs associated with late breeding arise due to a tight seasonal schedule. This obviously results from the individuals in the population growing beyond a size that allows completing the reproductive functions easily within the short arctic summer. A small body size is counteracted by a strong selective advantage of being large (Choudhury *et al*. 1996), and abandoning a clutch in time may be one of the mechanisms to combine a large body size with minimal survival costs.

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